ROLE OF INVERTEBRATES IN THE DECOMPOSITION OF OAK LITTER

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Invertebrates are of immense importance in soil formation and play a major part in improving soil fertility.

With rare exceptions, soils are abundantly populated by invertebrates, especially by the small arthropoda (collembola, ticks), roundworms (Nematoda) and protozoa. An area of 1 m^2 of soil may contain up to a million collembola and ticks, more than 14 million Nematoda, (19) and hundreds of thousands of protozoa in every gram of the surface soil (4).

One of the most important factors in soil formation and one of the stages in humus formation is the decomposition of organic substances (plant and animal residues) (9, 15). In this process invertebrates play a very important part.

Of major significance in the decomposition of dead plant residues are the ground molluscs, the Nematoda, the enchytrae, the rain worms, the myriapod Diplopoda, wood lice, the ticks Oribatei and Tyroglvphoidea, collembola and fly larvae. There have been several attempts at a quantitative estimate of the activity of particular species or groups of soil invertebrates in the decomposition of forest litter, mainly under laboratory conditions (6, 7, 12, 16, 17, 21, etc.). It is important to estimate the activity of invertebrates under natural conditions, excluding the part played by vertebrate animals in the litter decomposition but including the part played by bacteria and fungi. This was the purpose of the present work.

Location and Methods of Research

In 1958 we investigated the activity of soil fauna in the decomposition of oak litter in comparatively dry goutweed-infested oak stand on thick, humus-rich chernozems in the Central Chernozem Reservation near Kursk.

M.S. Gilyarov suggested using naphthaline in order to exclude the invertebrates from the decomposition process. Our own research has confirmed his finding that naphthaline drives away the animals and completely excludes them from taking part in the decomposition process, whereas if Kholodnyy et al. (14) and Fedorova (13) are correct it does not prevent the decomposition caused by the bacteria and fungi.

Kholodnyy and co-workers (14) set up tests in which they inoculated mineral gels with chernozem and podzolized forest soil aggregates. A variety of bacterial colonies very quickly appeared in the naphthaline vapors from the gel in the neighborhood of the soil aggregates. It was found that these microorganisms could destroy even the naphthaline itself.

The fact that in our own investigations we found pilei, which are one of the main fungus agents of forest litter decay (15), as well as bacteria developed even in the absence of naphthaline, indicates that decomposition caused by fungi and bacteria continues to occur in the presence of naphthaline. M. M. Zozulina, a microbiologist of the Central Chernozem Reservation, confirmed that bacteria of the same type as those found in ordinary litter were present in litter (oak leaves) treated with naphthaline for four months, by inoculating cultures on meat peptone agar.

Two series of tests were started in the second half of May in more or less identical plots of the oak stand, the first on litter which had already consolidated before the tests were set up and the second on leaves which had remained on the trees throughout the winter and been removed in spring before shedding.[1] A quantity of 373 g of spring-fallen leaves in air dry conditions was piled on soil which had been carefully cleared of old litter (according to unpublished figures obtained by Ye. A. Afanas'yeva and V. V. Gertsyk this is the average amount of litter per m^2 of oak stand in the reservation). In both series the litter on the soil surface was covered with wooden frames 1 m^2 in dimension, with walls 15 cm high, tightened with a caprone sieve with 2 x 2 mesh. The plants were left under these frames and as they grew up from under the sieve, the invertebrates could readily penetrate the frames and escape from them. In both series half the number of frames were kept as controls; from May 21 onwards naphthaline was poured into the experimental frames in such a way that the litter surface was always more or less covered by a thin naphthaline layer. The naphthaline volatalized fairly quickly in the open air and 2.5 kg per m^2 were used during the 140 days of the experiment.

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[1] Two varieties of oak (*Quercus robur* L.) are found in the Central Chernozem Reservation; one sheds its leaves in autumn, the other in spring.

A population count of the litter was taken once every 10 days in the test area but at a fair distance from the actual test points so as to avoid the influence of the naphthaline. The larger forms were counted by manual selection on 32 quarter-m² (50 x 50 cm) plots every 24 hours. The smaller population (ticks, collembola) were counted by means of eclectors set in the sun (10 samples to every 100 cm²).

Laboratory experiments (2 replicates) in treating the litter with Tipula scripta Meig., Sarmatiulus kessleri Lohm, and Tracheoniscus rathkei Brandt larvae were made at the same time, using leaves from the litter which had begun to decompose as the test material. A sample of leaves which had been thoroughly dried in the sun was placed in a crystal pan loosely covered with a lid and wetted with rainwater. A known number of invertebrates of the same species, which had been left without food for several days so as to clean out the intestines, was placed on these leaves. The animals were again left without food after they had been allowed to feed on the leaves and the excrements produced during this period were compared with those produced during the test period. The experiment was as a rule continued for 10 days. The animals were kept in a room at more or less constant temperature.

Invertebrates of the same species were reared in the laboratory at the same time for the purpose of obtaining a sufficient quantity of excrement for chemical analysis. The excrements were collected after the inverbetrates had been kept for 1-1/2 months and immediately dried. On the advice of M. M. Kononovaya the excrement was extracted with saturated solution of sodium fluoride (NaF solution was used in order to detect humic substances in the excrements).[2]

Role of Invertebrates in the Decomposition of Oak Litter

Three experimental and control counts were made in each series over a period of 140 days in the autumn (from May 21 to October 8), the leaves being carefully collected and dried. The results are given in Table 1.

In the first series (in spring a known quantity of leaves were taken from the trees and heaped on clean soil) 9% of the litter disappeared when the invertebrates were excluded and 55.3% when they contributed to the decay.

When the invertebrates are excluded, then the bacteria and fungi alone cause only about one-tenth of the oak litter to decompose, whereas more than half of it decays when soil animals are operating in conjunction with the bacteria and fungi.

The results of the second series confirm those of the first. As in the first series, also in the second (with the old, caked litter) where the original quantity of material was unknown, the amount of litter fall in the experiment (with the naphthaline) was found to be nearly twice as great as in the control. In the first series 339.3 g of leaves were left after decomposition without participation by invertebrates and 166.8 g after decomposition in which invertebrates

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[2] The work was done by a joint team consisting of Ye. A. Afanas'yeva, soil scientist, and A. M. Semenovaya-Tien-Shanskaya, geobotanist. The invertebrate determinations were made by T. S. Perel' (rain worms), I. Ye. Lokshina (myriapods), Ye. V. Borutskiy (wood lice) and N. P. Krivoshennaya (fly larvae).

Table 1

Role of soil invertebrates in the decomposition of oak litter

Series	Treatment	Original quantity of litter	Weight of litter remaining after 140 days	Amount of litter decayed in 140 days		Difference in the quantity of litter remaining in the experimental and control lots	
		Grams			Original quantity, %	Grams	Experimental quantity, %
First	Without invertebrates	373	339,3	33,7	9,0	172,5	100
Spring litter	Control (with invertebrates)	373	166,8	206,2	55,3		50,8
Second	Without invertebrates	?	470,1		—	228,4	100
Old litter	Control (with invertebrates)	?	241,7		—		48,6

Note: Comma represents decimal point.

Table 2

Litter population in oak forest of Central Chernozem Reservation in 1958 (number per m²)

Animals	21–22.V	31.V–1.VI	10–12.VI	20, 22–23.VI	10–11.VII	20–21.VII	2–4.X	20, 22.X
Dendrobaena octaedra Sav.	17,3	11,5	167,7	157,1	171,0	9,3	61,4	55,5
Others (mainly Eisenia rosea Sav.)	6,7	1,4	7,0	20,2	16,8	1,1	5,0	1,8
Total rain worms	24,0	12,9	174,7	177,3	187,8	10,4	66,4	57,3
Enchtreidae	80	70	200	250	330	30	1500	2570
Thread polypods	4,1	3,3	3,9	2,9	2,1	0,8	3,5	0,7
All diplopods	4,5	3,3	5,1	3,6	4,3	0,9	4,6	0,8
Wood lice	4,4	4,7	7,7	9,7	9,3	6,0	2,0	1,3
Leatherjacket larvae	1,5	1,9	2,1	3,8	2,0	1,3	0,1	0,9
All dipterous larvae	2,0	2,4	2,3	11,3	10,0	1,4	4,0	3,0

Note: The October Enchytreidae count was made by manual selection of 100-cm² samples (10 samples per count). The values for the preceding month were taken from the small animal count made with eclectors but gave slightly lower values. Manual selection from the 0.25-m² samples produced still lower values. Visual evaluation in autumn showed the Enchytreidae to be the most numerous.

Note: Comma represents decimal point.

took part. This gives a difference of 172.5 g or 50.8% of the quantity of leaves remaining after decomposition without participation by invertebrates. In the second series the difference was 228.4 g (470.1 less 241.7) or 48.6% of 470.1 g. The difference figures (50.8% and 48.6%) are therefore fairly close.

The fact that the condition of the control litter in regard to degree of decomposition in the second series of experiments (where the litter was caked and intact) and in the surrounding parts of the forest indicates that the natural course of decomposition was not affected by the presence of the frames over the leaf fall.

From the experimental values it can be inferred that the decomposition of oak litter by bacteria and fungi alone is slow. These values bear out the propositions that soil animals accelerate the decay of plant residues by breaking them down, partially digesting them, adding them into the soil along with excrements and bacteria and so forth (2, 4, 5, 8, 10, 16, 17). The microorganisms in turn promote the activity of soil saprophages; invertebrates are reluctant to eat fresh litter which has not been subjected to any microbiological decomposition at all; conversely the more the litter has been worked over by microorganisms, the more intensively it is consumed by animals (17, 19, 21). It follows that the activity of microorganisms in the process of plant residue decay is associated with that of invertebrates.

Among the larger soil invertebrates the main agents of oak litter decomposition in the Central Chernozem Reservation are the rain worms Dendrobaena octaedra Sav., the Enchytreidae, the thread polypods (Sarmatiulus kessleri Lohm., Chromatoinlus rossicus Tim., Brachyiulus jawlowski Lohm.), the wood louse Tracheoniscus rathkei Brandt and the larvae of the leatherjacket Tipula scripta Meig.

The laboratory tests showed that the daily consumption of oak leaf litter (converted to dry weight) per day was: by older Tipula scripta larvae (pre-experiment weight 136-191 mg), 10-15 mg; adult Sarmatiulus kessleri (weight 202-245 mg), 10-11 mg; adult Tracheoniscus rathkei (weight 43-45 mg), 2-3 mg; animals with a heavier body weight per unit mass consumed less food.

The count of litter population (Table 2) showed an average of approximately two leatherjacket larvae, three thread polypods and seven wood lice per m² over the two months from the end of May to the end of July. Calculations made on the basis of the amount of litter consumed showed that in the two summer months alone these animals could destroy at least 5 g of oak litter (converted to dry weight) per m² of forest.

The population in those species of invertebrates with which the laboratory experiments were concerned was low; these species, therefore, had no major importance in the decomposition of the oak litter in the reservation, where the main role was played by the rain worms Dendrobaena octaedra (up to 170 per m² of litter), the Enchytreidae (up to 2570), the ticks (up to 22,380).[3] and the collembola (up to 6110). These values are an underestimate as a result of imperfections in the counting methods used, which did not allow all the animals encountered in the soil and litter to be taken into account. In addition to the animals enumerated, land molluscs, nematodes and other decomposition agents not counted by us also took part in the decomposition of the oak litter. The combined activity of all invertebrates together with bacteria and fungi had a similarly important effect in the experiments described.

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[3] According to determinations made by Yu.V. Byzovaya, who studied soil ticks in the Central

Weather conditions promoted decay of the litter. In summer and autumn of 1958, there were comparatively few days when the litter was completely dried, with the result that the animals left the litter layer and returned to the soil. Fairly low temperatures, frequent and fairly abundant rainfall and morning dews in the intervals between showers kept the litter damp over a long period. Only in the period from late May to the beginning of June and at the beginning of the second half of July was the weather dry and warm; the invertebrates then stayed in the litter (Table 2). On May 31 and June 1, for example, despite the increased population (as a result of spring growth) the count for nearly all the animals was lower than in the preceding count (May 21-22). This was particularly striking in the case of the rain worms: in 10 days (June 10-21) when there was continuous rain and constant temperatures, the number of rain worms in the litter sharply increased. On July 20-21, after a long break in the rainfall and relatively high temperatures rising from day to day, the number of rain worms in the litter again sharply declined. The maximum quantity of rain worms was observed in the first 10 days of July, whereas the maximum quantity of nearly all the other larger animals responsible for litter decay was observed in the last 10 days of June. It must be noted that in 1958 the development of the invertebrates was very late (the Tipula scripta Meig larvae, for example, are according to Savchenko (11) usually found from early spring until the beginning of June).

Among the small arthropoda, the maximum tick population was observed at the beginning of the second 10 days in June and the maximum collembola population at the beginning of the last 10 days of that month (Table 3).

Role of Invertebrates in the Humification of Oak Litter

Soil invertebrates play not only an indirect but also a direct role in the decomposition of organic matter. "In the process of animal metabolism complex organic substances and organic residues are broken down. Some representatives of the soil fauna are capable of hydrolyzing not only the readily absorbed carbohydrates, fats and proteins, but also much more resistant substances like cellulose, keratin and chitin. As a result of metabolism various organic substances are converted into plant-available compounds (carbon dioxide, water, ammonia) or readily mineralized compounds (urea, uric and hippuric acids, guanine). Many salts are also excreted in the free state —the chlorides and phosphates of potassium, magnesium, sodium, calcium, etc."(4) In addition, humic substances, the importance of which is well known, are formed in the digestive processes of soil animals.

Franz and Leitenberger (20), who set up specific tests to investigate the excrements of a series of soil invertebrates, confirm that a humus-like substance, which they believe to be a first stage in humus formation, is formed intestinally directly from fresh litter that has not yet been subject to microbiological decomposition. These investigators determined the degree of humification from the quantity of acetyl bromide-insoluble matter, using the colorimetric method, comparing the excrements with the original food. They believe that in the process of digestion a humic substance is synthesized, a substance which is insoluble in acetyl bromide being converted into one which is soluble. Quoting other investigators, they state that even animals which feed on green vegetation are capable of producing humic substances.

These inferences are borne out by the findings of Dunger (18), who studied how the litter changes in the intestine of certain species of polypods and wood lice, by spectrophotometry of an alkaline (NaOH) extract from the excrements. Dunger chose groups of animals, Diplopoda and Isopoda, which were not suitable enough to settle the question of humus formation. By means of detailed histological investigations he found that animals belonging to these groups do not easily digest plant tissues. Our own investigations provided further evidence of this. Van der Drift and Kubiyena (quoted by Franz (19) also noted that

Table 3

Tick and collembola population in oak forest litter in the Central Chernozem Reservation in 1958 (thousands per m²)

Animals	22.V	1.VI	11.VI	22.VI	3.VII	12.VII	21.VII	1.X
Ticks	16,08	19,29	22,38	20,37	18,70	13,60	8,56	14,95
Collembola	3,27	4,21	4,11	6,11	4,32	4,55	2,28	4,86

Note: Comma represents decimal point.

Chernozem Reservation in 1957, tick-saprophages (Oribates-Tyroglyphoidea) make up about 80% of all the tick population in the forest litter (the mean total tick population in May-June was 26.5 thousand per m2, of which 21.5 thousand were saprophages).

digestion of plant material by the polypods Dipopoda and the wood lice was incomplete. It is therefore not surprising that Dunger detected only a slight increase in the amount of humic acids in the excrement of the animals he studied as compared with the food consumed.

What is this first stage in humus formation referred to by Franz and Leitenberger? It may possibly consist of those amorphous brown humic substances produced by Kononova (8) in experiments on the decomposition of alfalfa roots by microorganisms and larvae of the fly Sciara sp. which he calls "prehumic."

When the extracts we obtained from the initial material (litter which had been subjected to microbiological action), using sodium fluoride, were compared with the excrements of Sarmatiulus kessleri, Tracheoniscus rathkei and Tipula scripta, it was found that humic matter formation in the thread polypod and wood louse intestines was poor. The color of the excrement extracts was almost as bright as that of the original leaves. The extract from the excrements of leatherjacket larvae was distinguished by a much darker color.

What has been said previously about the role of soil animals in humus formation does not contradict the experimental finding that the humic matter content in the excrements of thread polypods and wood lice is not greater than that in the litter. This explanation is: first, that the food taken in by these animals is incompletely digested; and secondly, that of all tree species, except the beech, the oak produces the least digestible leaf for litter saprophages, including the thread polypods and wood lice and even, as Dunger confirms (17), for microorganisms. Oak leaves are less readily consumed by all animals and produce a much smaller quantity of new humus in the excrement than do other more easily broken down leaves such as those of the alder, ash, basswood and other trees (17, 19). Two examples may be adduced in support of this: 1) according to investigations by Volz (22), in Germany, alder forest litter completely disappears as early as the end of April, whereas in oak-ash forests the oak leaves decay as a rule during the 12 months following the defoliation period and the ash leaves decay a good deal earlier. 2) in the experiments by Franz and Leitenberger (20) mentioned previously, the excrements of the earthworm Lumbricus rubellus Hoffm., fed on oak leaf fall contained only half as much newly formed humic matter as that of the same animals fed on black alder leaves and only one-third as much as that of those fed on hazelnut leaves.

Dunger (18) fed polypods and wood lice, through the winter, oak leaves and established that there was a slight reduction in the amount of humic matter in the excrement of the first and a very slight increase in that of the second in comparison with the original material. It can therefore be said that thread polypods and wood lice do not themselves create humic substances in the course of oak litter decomposition and play only an indirect part in humus formation in the oak stands of the reservation, if we do not consider the possibility of their forming these substances from the litter from herbaceous plants and other tree species and shrubs typical of the oak stand.

The picture is different in the case of Tipula scripta larvae. Here the excrements understandably show a substantial increase in the amount of humic matter, since these belong to a group of insects which are capable of digesting cellulose (2, 3). Unlike the thread polypods and wood lice, in which the intestine is in the shape of a straight tube, these animals possess a digestive system of peculiarly complex arrangement. In addition to other complications of the digestive system, larvae which break down cellulose have an extremely dilatated posterior intestine (the Lamellicornia), or even a peculiar and relatively extensive excrescence at the beginning of the posterior intestine (Tipula) forming a so-called "zymotic camera" in which, as it would seem from Werner's findings quoted by Gilyarov (3), cellulose is broken down with the help of microorganisms. The activity of these microorganisms is undoubtedly connected with the animals' digestive processes. Microorganisms are active in the animals' intestines and depend on the latter's vital activity. The formation of humic substances occurs as a result of the combined activity of invertebrates and microorganisms. Leatherjacket larvae accordingly themselves take part in creating humic substances even in connection with the decomposition of oak litter.

V. V. Ponomareva analyzed the excrements of thread polypods, wood lice and leatherjacket larvae collected by us. The method used, however, did not make it possible to find the difference in the humic matter content in the leatherjacket larvae excrements as compared with those of the thread polypods and wood lice. The qualitative composition of the organic matter in the excrement was very similar to that in the original oak leaves (from the forest litter).

From this it may be concluded that different animals produce humic substances in different amounts, depending on the type of food they eat.

An immense amount of excrement falls into the soil. It is known from the foreign literature cited by Franz and Leitenberger (20) that the upper layer of many forest soils has an exclusively coprogenic character. This layer is continuously built up from above and drawn down into the soil from below.

Organic residues falling into the soil in the form of excrement after primary processing by invertebrates and intermingled with mineral particles is subjected repeatedly to the action of microorganisms and repeatedly passes through the intestines of various animals (coprophages and saprophages). with the result that one way or another the organic material alters, in the direction of humification.

Received April 20, 1959

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